

INFLUENCES OF SEX AND WEATHER ON MIGRATION OF MULE DEER IN CALIFORNIA

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ABSTRACT—I examined differences by sex and influences of weather on timing and patterns of migration of Rocky Mountain mule deer (*Odocoileus h. hemionus*) in the eastern Sierra Nevada, California, during 1954-57. Deer initiated spring migration from the winter range at about the same time in all years and made extensive use of holding areas at intermediate elevations. Radio-telemetered deer showed strong fidelity to summer ranges over as many as four years. Fall weather produced different patterns of fall migration. Storms during October produced a pulsed migration, in which most animals migrated to the winter range during or soon after the storm; in a year without a storm, fall migration was gradual. Despite the influence of storms on the pattern of fall migration, the median date of fall migration by females did not vary over years; however, among males it was later in a year without fall storms.

Key words: migration, mule deer, *Odocoileus hemionus*, sex differences, weather, radio telemetry, California.

Seasonal migration is common among a wide variety of vertebrates (Baker 1978), including large terrestrial mammals (McCullough 1985, Fryxell and Sinclair 1988). Migration ultimately contributes to individual reproductive success (Baker 1978). Proximally, however, migration is related to the seasonal availability of resources (Sinclair 1983, Garrott et al. 1987). Migration is a common phenomenon among mule deer (*Odocoileus hemionus*) in the mountainous western United States, and various studies have described aspects of mule deer migration (Russell 1932, Leopold et al. 1951, Gruell and Papez 1963, McCullough 1964, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). However, questions remain as to the influence of proximate factors, especially weather, on the timing of migration. In addition, because studies of mule deer involving radio-telemetry rarely have included males (e.g., Garrott et al. 1987, Loft et al. 1989), little is known of differences between the sexes in migration patterns.

My objectives were (1) to describe the timing and pattern of seasonal migration of mule deer in the eastern Sierra Nevada, California; (2) to test the hypotheses that there were no differences by sex or year in the timing and pattern of migration and degree of summer-range site fidelity; and (3) to relate observed migration patterns to other aspects of the ecology of these animals.

STUDY AREA

The Sierra Nevada is a massive granite block tilted toward the west, extending for 600 km in a generally northwest-southeast direction (Storer and Usinger 1968). The west side of the mountain range slopes gradually for 75-100 km, from the foothills near sea level to the crest at 3000-4500 m. The eastern Sierra Nevada is more narrow and steep than the west side, with frequent elevational changes of 3000 m in <10 km.

A population of 3000-6000 Rocky Mountain mule deer (*Odocoileus h. hemionus*) winters at the base of the eastern escarpment of the Sierra Nevada in Round Valley, Inyo and Mono counties, California, about 15 km west of the town of Bishop (Fig. 1). An area of about 90 km² of Round Valley is used by mule deer as winter range, at elevations from about 1450 to 2100 m. Pine Creek forms the dividing line between what is termed the Sherwin Grade (SG) deer herd to the north and the Buttermilk (BM) herd to the south. These deer are hunted under bucks-only regulations, and posthunt adult sex ratios of 7-12 males:100 females occurred during this study (California Department of Fish and Game, Bishop, California).

As winter storms from the Pacific Ocean rise up the western slope of the Sierra Nevada, they deposit moisture, leaving a much more arid rain shadow on the east side. Precipitation in the

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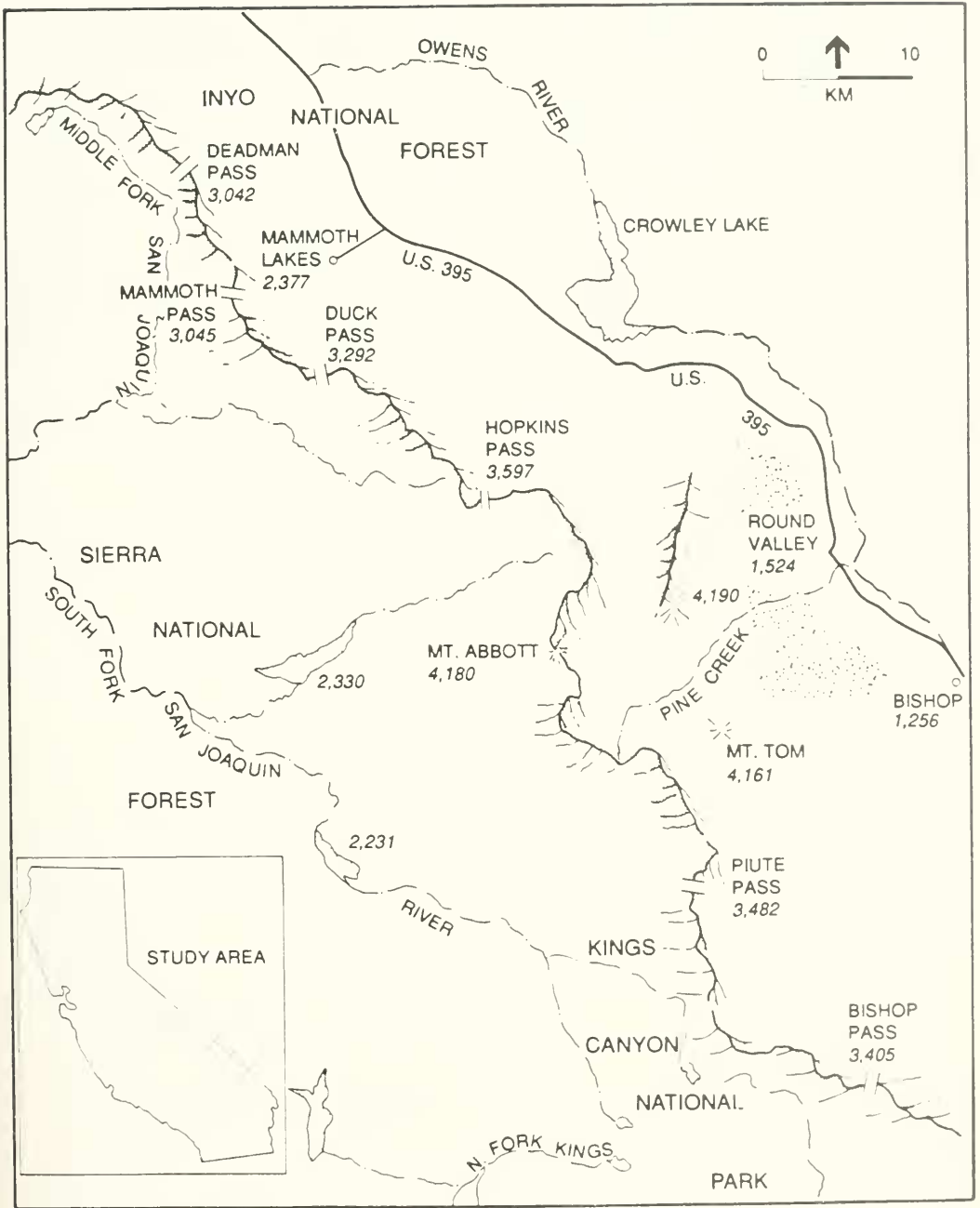


Fig. 1. Map of the study area showing the deer winter range as the shaded area in Round Valley; the crest of the Sierra Nevada is from northwest to southeast, with elevations (m) of selected peaks and major passes.

area ranges from an annual mean of 14.5 cm at the Bishop airport at 1240 m to 40.6 cm at 2560 m in Pine Creek Canyon (Vaughn 1983, National Oceanic and Atmospheric Administration 1987). Precipitation is strongly seasonal,

with about 75% of the annual total occurring between November and March. Summers are hot, with daytime temperatures in July often $>37^{\circ}\text{C}$. January is the coldest month, with an average temperature of 4°C and frequent

nighttime lows of <-15 C. Potential evapotranspiration is 66.8 cm, or more than four times the mean precipitation.

Vegetation on the winter range is typical of the Great Basin Desert and conforms to the sagebrush belt of Storer and Usinger (1968). Shrubs are dominant, and blackbrush (*Coleogyne ramosissima*), rabbitbrush (*Chrysothamnus* spp.), big sagebrush (*Artemisia tridentata*), and antelope bitterbrush (*Purshia tridentata*) are most common. Deer summer ranges are on both sides of the Sierra crest, at elevations from about 2200 to >3600 m (Kucera 1988), and include the sagebrush, jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*P. murrayana*)—red fir (*Abies magnifica*), subalpine, and alpine belts (Storer and Usinger 1968).

Livestock use of deer winter range was light, consisting of 129 animal-unit-months of use by cattle, restricted to part of the SG range from 1 April to 15 October (U.S. Department of the Interior 1990). Use of deer summer areas by livestock (including horses, cattle, and sheep) varied from very heavy in more accessible locations on the east side of the mountain range to none at higher elevations and more remote areas.

METHODS

Fieldwork was conducted from January 1984 through May 1987. Deer were captured on the winter range January through March 1984 and January and February 1985 with a variety of methods including Clover traps (Clover 1956) baited with alfalfa, drive nets using a helicopter, and remotely triggered drop-nets; net guns fired from a helicopter and tranquilizer darts also were used to capture selected males. Deer captured in 1984 in Clover traps were chemically immobilized with Rompon (xylazine hydrochloride), the effects of which were reversed with yohimbine after handling (Jessup et al. 1985). Deer were captured also during May 1984 and 1985 with tranquilizer darts on a spring migration "holding area" (Bertram and Rempel 1977) about 50 km north of the winter range. This is an area where deer congregate for 2–6 weeks before continuing to areas occupied during the summer.

I fitted 5 males and 9 females from the BM winter range, 7 males and 10 females from the SG winter range, and 10 females captured on the spring holding area with radio collars

(Telonics Inc., Mesa, Arizona). All deer were ≤ 2.5 years of age. I attempted to distribute capture efforts throughout accessible areas to minimize biases in the marked sample. I selected females for telemetry to include all age classes of adults; however, I selected males to receive radio collars on the basis of large size and relatively old age. I excluded smaller, younger males because of concerns arising from body growth; males do not approach maximal neck circumference until about 4 years of age (Anderson 1981), and this, combined with seasonal neck swelling during rut, could result in injury caused by radio-telemetry collars. Older males have achieved nearly maximum body growth; I allowed for seasonal neck swelling by attaching the nonexpandable collars with a circumference 20–25% larger than the animal's neck circumference after rut, measured midway between head and shoulders. I noticed no serious problems resulting from the use of radio collars on male deer in this study, although after a year or two, some fur appeared to be rubbed off the backs of the necks; a similar situation occurred with telemetered females. Collars on the males moved toward the head when the necks swelled during rut and hung loosely at other times.

While animals were on the winter range, I determined at least once per week, and usually more often, whether each radio-marked animal was on the BM or SG winter range by observing the direction of transmitter signals received from standard locations. These data were supplemented by additional radio locations and visual locations as observers moved through the winter ranges. During spring and fall migrations, and during summer, locations of telemetered deer were determined from a fixed-wing aircraft, from a vehicle, and from the ground. During the spring, locations were determined several times per week until the animals crossed the crest of the Sierra. Due to the remoteness of most summer ranges in roadless wilderness areas, frequency of locations of animals, determined from the air and the ground, on the west side of the Sierra Nevada was approximately twice per month. Of 42 deer that reached summer ranges, I located 38 from the ground.

Twenty-two deer were followed for more than one summer. Of these, 10 (45%; 1 male, 9 females) were located in two consecutive summers, 9 (41%; 3 males, 6 females) in three consecutive summers, and 3 (14%; 1 male, 2 females) in four consecutive summers. For

these animals I expressed fidelity to summer range as the greatest linear map distance between mean locations in consecutive summers (1 July–7 September). During the fall, locations of animals were monitored from the east side of the Sierra crest at least several times per week, and frequently daily. I could thus determine, within several days and often within one day, when telemetered deer from the west side of the crest crossed to the east side.

I divided annual migration into three periods: (1) leaving winter range, defined as ascending to an elevation >2100 m; (2) crossing the Sierra Nevada crest in spring; and (3) crossing the crest in fall. The last two apply only to those animals ($n = 34$) that summered west of the crest. Because of logistic difficulties in locating animals on the west side of the crest, I did not attempt to determine precisely when animals crossing the crest reached their summer ranges. The steep eastern slope of the Sierra Nevada provided the opportunity to determine the presence or absence of a radio-marked animal on the east side with little error. In situations in which I could not determine an exact date of crossing, I estimated the date as the midpoint of the interval in which I did and did not receive a signal.

For analysis I determined frequencies of movement by week during an 8-week period of leaving the winter range beginning 1 April, a 7-week period of crossing the crest in spring beginning 15 May, and an 11-week period of crossing the crest in fall beginning 11 September. I used the Kolmogorov-Smirnov test with chi-square approximation (Siegel 1956) to test for sex differences in the timing of these components of migration. Steep mountains on the west side of Round Valley constrained movement off the winter range to northerly or southerly routes; I tested for sex differences in the direction (north or south) of migration from the winter range with the binomial test (Zar 1984:591). I expressed temporal patterns of fall migration as the percentage of radio-marked deer in an annual sample crossing the crest during any week. I tested for differences among years in the largest weekly percentage crossing the crest in any year with the Z-test (Zar 1984:396).

From April through June of 1985, 1986, and 1987, commencing as soon as snow conditions permitted, deer were counted from a vehicle along a standardized route of 11 km that passed

through a major spring holding area located 1–8 km south of the town of Mammoth Lakes, approximately 50 km north of the winter range. These weekly surveys began 30 minutes before sunrise, and direction of travel was alternated on consecutive surveys.

Daily precipitation in the fall was measured at the U.S. Forest Service (USFS) weather station at the Mammoth Lakes Ranger Station, Inyo National Forest, Mammoth Lakes, California, at an elevation of about 2400 m. Winter snowfall totals were from the USFS weather station on Mammoth Mountain, at about 2940 m.

RESULTS

Spring Migration

From 1984 to 1986 the first radio-marked deer left the winter range during the first or second week of April in any year; in the same years the last radio-marked deer left during the second, third, and fourth weeks of May. For females the median departure date from the winter range was during the third, second, and third weeks of April 1984–86, respectively; for males, the median was during the second week of May and second and third weeks of April, respectively. The frequency differences by sex in weekly migration approached statistical significance ($X^2 = 5.94$, $df = 2$, $.05 < P < .10$).

Of the 17 telemetered deer from the BM range, 10 (3 of 8 males, 7 of 9 females) migrated north, through the SG range, to reach their summer range; 5 males and 2 females moved south. Of the 17 deer telemetered on the SG range, 15 (5 of 7 males, 10 of 10 females) migrated to the north; 2 males went south. Overall, more ($P = .0003$) females migrated north ($n = 17$) than south ($n = 2$). Analysis by herd showed a significant difference ($P = .0001$) in migration direction among SG females ($n = 10$); the difference among BM females ($n = 9$) approached statistical significance ($P = .07$). There were no significant differences among males in migration direction, either with all males combined ($n = 15$, $P = .196$), or by herd (BM: $n = 8$, $P = .22$; SG: $n = 7$, $P = .16$). Of the 10 females captured on the spring range, 4 wintered on the BM range, 5 wintered on the SG range, and 1 died before the fall migration.

Holding Areas

After leaving the winter range, telemetered deer moved to higher-elevation holding areas at

2200–2400 m on the east side of the Sierra Nevada. Hundreds of deer already were present on the first road surveys of the spring, and patterns of occurrence were similar in all years (Fig. 2). Largest numbers were counted in late April and early May; numbers then decreased through mid-June as deer moved to summer ranges. During early spring a portion of the wintering animals also foraged in irrigated meadows immediately adjacent to the winter range in Round Valley.

Diminution of deer counted on the holding area was reflected by an increase in deer crossing the crest to summer ranges. Of the radio-marked deer that summered west of the crest, the first crossed the crest during the third or fourth week of May in any year, and the last crossed during the third or fourth week of June. There were no sex differences in timing of spring crossing ($\chi^2 = 3.50$, $df = 2$, $P > .10$). The median for both sexes in all years was the first week of June.

The temporal uniformity over years in leaving the spring holding area for summer ranges occurred despite greatly different snow conditions. In the winters of 1983–84, 1984–85, and 1985–86, the USFS recorded total snowfalls of 671, 767, and 1021 cm, respectively, on Mammoth Mountain, geographically close and at an elevation similar to the passes that migrating deer crossed to reach summer ranges on the western slope. Despite these differences in snowfall and consequent snowpack at higher elevations, no differences in the timing of spring migration were evident. The snowfall of winter 1986–87 was only 246 cm, or less than one-quarter of that of the previous year. Although the sample size is small, the median week that three radio-marked males and two radio-marked females crossed the crest in the spring of 1987 was the same as the previous year, the first week of June. Thus, the amount of snow on the ground did not appear to influence the timing of migration over the Sierra crest in the spring.

Summer Range

Of the 32 deer captured on the winter range that reached summer ranges, 28 (87.5%) crossed the Sierra crest and summered on the west side. Summer range locations of these deer, plus those of deer captured on the spring range, extended from the headwaters of the Middle Fork of the San Joaquin River south throughout the upper San Joaquin River drain-

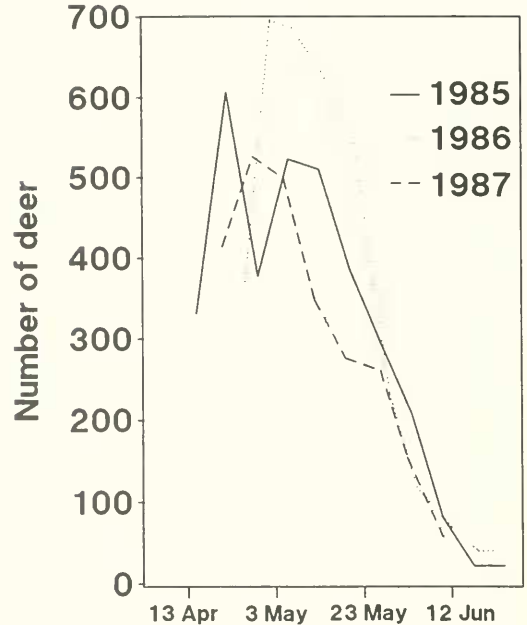


Fig. 2. Number of mule deer counted from a vehicle on standardized weekly surveys at dawn through a spring holding area near the town of Mammoth Lakes, Mono County, California, 1985–87. Surveys began in the spring when snow conditions made the roads passable.

age above about 2134 m into the North and Middle forks of the Kings River (Kucera 1988). Two males and 4 females summered on the east side of the Sierra, from Mammoth Pass on the north to the North Fork of Bishop Creek on the south. Thus, an area nearly 100×25 km served as summer range for deer from the BM and SG herds.

Summer Range Fidelity

Distances between summer ranges of 22 deer located in consecutive years averaged 0.7 km (range = 0.2–4 km) for both males ($n = 5$) and females ($n = 17$). Only 1 deer, a female, was >1 km from a previous location in successive summers; she spent her second summer about 2.5 km from her first, and her third and fourth about 1.5 km farther away.

Fall Migration

In 1984, 1985, and 1986 the first radio-marked deer crossed to the east side during the first week of October and second and fourth weeks of September, respectively; all were females. The last crossed during the fourth week of October and second and fourth weeks

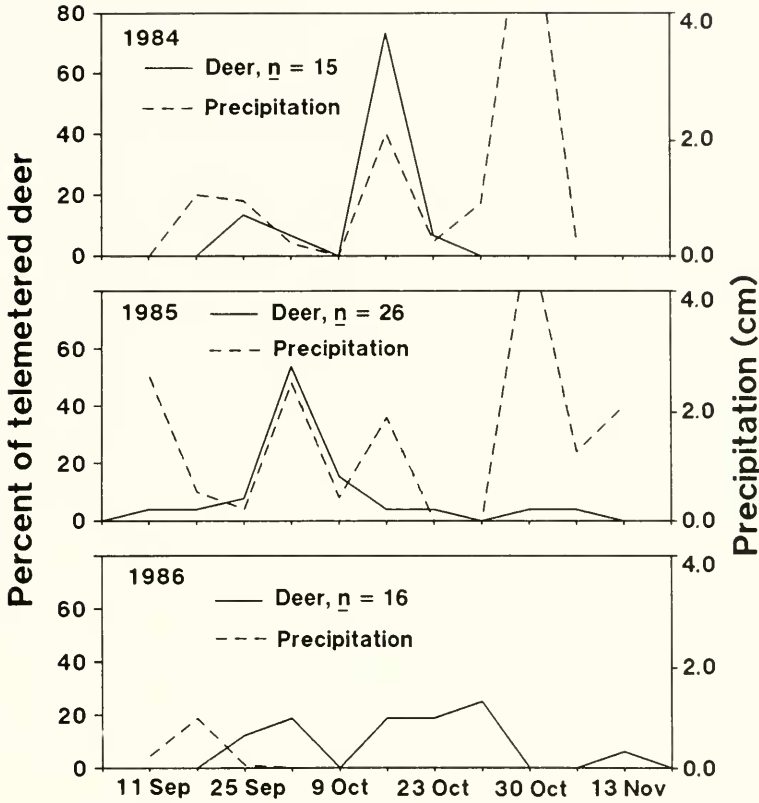


Fig. 3. Percentage of telemetered mule deer per week crossing the crest of the Sierra Nevada, Inyo and Mono counties, California, and weekly precipitation measured at the town of Mammoth Lakes, Mono County, in the fall of 1984–86.

of November; all were males. In 1984 and 1985 the median week of crossing the crest was the same for both sexes, the third and second weeks in October, respectively. In 1986 the median for females was the third week in October, but was two weeks later for males ($X^2 = 18.72$, $df = 2$, $P < .001$).

Length of time during which fall migration occurred also varied among years. In 1984, 11 of 15 (73%) and, in 1985, 14 of 26 (54%) telemetered deer, including both sexes, crossed the crest in a one-week period. These proportions were not different ($Z = 1.2$, $P > .11$). However, in 1986 no more than 4 of 16 (25%) radio-marked deer crossed the Sierra crest in any week. This proportion was smaller than those of the previous two years ($Z = 2.45$, $P < .007$), indicating that in 1986 there was no mass movement of deer in a short time period.

Differences among years both in timing and in pattern of fall migration were related to the presence or absence of major fall storms (Fig. 3). In 1984, 1.8 cm of precipitation in the form

of about 20 cm of snow was recorded on 17 October at Mammoth Lakes; no doubt snow at the passes (400–1500 m higher) used by migrating deer was much deeper. This storm was accompanied by a rapid movement of radio-marked deer over the crest and to the winter range within a few days. Earlier storms, which resulted in virtually no snow at the recording station, did not trigger movement. In 1985, shortly after a storm on 7 October, there was another rapid movement of deer over the crest. The remaining deer appeared gradually on the east side of the crest through 13 November, when the last radioed animal, a male, migrated over the crest following a major winter storm. In both 1984 and 1985 I saw dozens to hundreds of deer migrating simultaneously with the telemetered animals, and many tracks and deep trails in the snow were evident. In 1986 there were no major fall storms. Migration was gradual and unpunctuated by any rapid, mass movements (Fig. 3). In all cases deer returned to the

winter range (BM or SG) occupied in previous years.

DISCUSSION

In this study the timing of mule deer migration from the winter range did not differ among years. This occurred despite large differences in animal condition and vegetation growth measured on the winter range (Kucera 1988). One explanation may be that these deer had well-defined spring holding areas where they could predictably obtain nutritious forage, available even in years of heavy snowfall such as 1986, when hundreds of deer were on the holding area when counts began (Fig. 2).

Adult males may leave the winter range somewhat later than females, as reported from western Colorado (Wright and Swift 1942). Given the demands of pregnancy, females might be under greater nutritional stress than males, and if better forage conditions exist on spring ranges, females may tend to leave the winter range sooner to take advantage of them. Garrott et al. (1987) reported that spring migration of female mule deer in northwest Colorado varied between years by as much as one month, and they attributed these differences to the severity of winters and consequent energetic demands on deer. Bertran and Rempel (1977) reported that California mule deer (*O. h. californicus*) on the western slope of the Sierra Nevada varied the timing of their spring migration by two weeks, and attributed this to differences in plant phenology both on the winter range and along the migration route. Loft et al. (1989) also reported a similar relationship between initiation of spring migration and amount of snow and stage of plant growth in the western Sierra Nevada.

In my study most telemetered females migrated from the winter range to the north; males showed no significant selection for direction. I contend that this sex difference is a product of local geomorphology and land management patterns. Animals moving north had access to an extensive area of the west slope of the Sierra Nevada on national forest lands at elevations of 2200–2800 m. Animals moving south had access to summer range in King's Canyon National Park at higher and steeper, and thus more barren and less vegetated, elevations (Kucera 1988). The presence of more and better summer range to the north explains why

most deer of both sexes would migrate to the north. However, those animals migrating to the north were in areas open to hunting both on their summer ranges and along the migration routes. That telemetered males showed no apparent selection for migration direction, whereas most females migrated to the north, probably resulted from the higher hunting mortality of males summering to the north, and the absence of hunting in the national park. Although as many males as females would be expected to migrate to the north, the higher mortality of adult males moving north could explain the apparent pattern of no directional preference. Because older males are disproportionately reproductively successful (Kucera 1978, Geist 1981, Clutton-Brock et al. 1982), the national park may act as a refuge for a large proportion of the most reproductively successful males.

Deer in this study made extensive use of holding areas in the spring (Fig. 2), which may be beneficial because of higher elevation, greater precipitation, and absence of winter feeding. Vegetation in these holding areas was largely sagebrush scrub (Muniz and Keck 1959), a common vegetation type in the eastern Sierra Nevada. These areas are among the last large areas with vegetation suitable for deer present in the spring before the deer cross the Sierra crest. Large aggregations of deer on the holding areas may result from animals simply collecting in these areas for several weeks before ascending over the crest. Bertran and Rempel (1977) and Loft et al. (1989) described a similar pattern of use of spring ranges in the western Sierra Nevada and emphasized the importance of these holding areas in providing herbaceous forage. Further, Bertran and Rempel (1977) reported that spring holding areas typically occurred at the base of an abrupt elevation change, which was true in my study.

Timing of movement off the holding area and over the crest in spring did not differ among years or between sexes, suggesting that animal condition or vegetation did not greatly affect this stage of migration. The passes had snow in all years of study when deer crossed, but snow depths differed greatly. However, by spring snow was consolidated, enabling deer to walk over the surface.

In 1951 Jones (1954) found that BM deer began moving off the winter range about 1 April, and began crossing a nearby pass about 15 May.

This agrees well with the present observations made more than three decades later. In the western Sierra Nevada, Russell (1932), Leopold et al. (1951), Bertram and Rempel (1977), and Loft et al. (1989) described spring migration as an "upward drift" of deer, controlled by the receding snowline and spring plant growth. My study showed a different pattern in the eastern Sierra Nevada. The upward movement of deer was blocked by the abrupt elevation change of the mountains. On the more gently sloping west side, deer can follow spring gradually up slope. On the abrupt east side, the need to cross high-elevation passes prevents such a pattern.

The strong fidelity to specific summer home ranges shown by individual deer in this study is characteristic of mule deer (Ashcraft 1961, Gruell and Papez 1963, Robinette 1966, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). With few exceptions, both males and females returned to the same summer home ranges, and winter ranges, for as many as four consecutive years.

The temporal pattern, pulsed or gradual, of the fall migration in the eastern Sierra Nevada is largely determined by weather, particularly snowstorms. In both years with significant snowfall in October, radioed deer moved rapidly and in a pulsed fashion from summer ranges to the winter range (Fig. 3). In a year without significant fall storms, movement was gradual, and males migrated significantly later than females. Previous studies discussed the relationship of snowstorms to fall migration (Russell 1932, Dixon 1934, Leopold et al. 1951, Richens 1967, Gilbert et al. 1970), although some cases were based on anecdotal evidence. Bertram and Rempel (1977) stated that deer on the west slope of the Sierra Nevada moved in anticipation of fall storms, but I found no evidence of this. Garrott et al. (1987) speculated that in northwest Colorado deer moved not because of snow, but to maximize the quality of their diets prior to winter. Differences in details of deer migration apparent between my study and studies in the western Sierra Nevada and in northwest Colorado indicate that deer migration can be influenced by local conditions.

Females may be constrained in their timing of fall migration by the nutritional and energetic demands of lactation and smaller body size, by the inability of fawns to cope with severe fall conditions, or both. Males do not have the same energetic, nutritional, or parental constraints.

Additionally, as consequence of hunting regulations, those males that do migrate early are likely to be killed.

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